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INFERRING THE ABSENCE OF A SPECIES—A CASE STUDY OF SNAKES

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Abstract: Though the presence of a species can be unequivocally confirmed, its absence can only be inferred with a degree of probability. I used a model to calculate the minimum number of unsuccessful visits to a site that are necessary to assume that a species is absent. The model requires the probability of detection of the species per visit to be known. This probability may vary depending on habitat, year, season, the area surveyed, the population size of the species, and the observer. I studied 3 European snake species—asp viper (*Vipera aspis*), smooth snake (*Coronella austriaca*), and grass snake (*Natrix natrix*)—over a 5-yr (1994–1998) interval, and made 645 visits to 87 sites during their activity periods. I used a generalized logistic regression approach with random effects for years and sites to (1) estimate the probability of detection of these species from sites known to be occupied, (2) test factors affecting it, and (3) compute the minimum number of times that a site must be visited to infer the absence of the particular species. Probability of detection for all species was heavily influenced by an index of population size. For *V. aspis*, probability of detection increased from 0.23 to 0.50 and 0.70 in small, medium, and large populations, respectively. Similarly, probability of detection increased from 0.09 to 0.45 and 0.56 in small, medium, and large populations of *C. austriaca*, respectively, and from 0.11 in small to 0.25 in medium and large populations of *N. natrix*. Probability of detection also varied across months for all 3 species, among habitat types (*C. austriaca* only), and from year to year (*N. natrix* only). Sites with unknown occupancy status conservatively may be assumed to be occupied by small populations. I calculated that such sites need to be surveyed 12, 34, and 26 times for *V. aspis*, *C. austriaca*, and *N. natrix*, respectively, before assuming with 95% probability that the site is unoccupied. These results suggest that some species may be more widespread than thought. However, to ascertain the presence of such species at a site, search efforts need to be intensive.

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Key words: asp viper, *Coronella austriaca*, Europe, generalized linear mixed model, grass snake, Jura mountains, monitoring, *Natrix natrix*, probability of detection, rare species, snakes, smooth snake, *Vipera aspis*.

The extinction of species is a major concern in ecological conservation (Vitousek 1994). However, extinction is not readily ascertainable. For elusive species, failure to detect specimens at a site does not necessarily equate to their absence. While the presence of a species may be proven by encountering ≥1 specimen, its extirpation can never be concluded with absolute certainty. Only probabilistic statements about its likelihood of absence can be made.

Wildlife managers and conservation biologists must be reasonably sure that the presence or absence of a species has been correctly determined. Metapopulation theory can be tested only if the distributional pattern of the study species has been well established (Hanski et al. 1996, Wahlberg et al. 1996). In conservation biology, it may be critical to know if a species truly has become extinct at a site or whether it merely has been overlooked (Dennis et al. 1991, Pounds and Crump 1994, Drost and Fellers 1996, Hecnar and McCloskey 1997). In many situations, it may be difficult to ascertain whether a rare species has been extirpated or is present in small numbers or at a very low density. If a species' presence has been overlooked, an important locale for that species may not receive protection or proper management, and local extinction could occur.

A common method used to check for the presence of a reptile species is to visit the site until ≥1 specimen has been found, or to abandon the search after a number of unsuccessful visits (but see a study by Reading 1997 for an alternate view). For example, in governmental reptile inventories in Switzerland, biologists visit sites only 1–4 times (e.g., Dusej and Billing 1991, Hofer 1991, Flückiger and Peltier 1999, Müller and Dusej 2000). If a species is undetected, it is concluded that the site is unoccupied. However, there is no way of knowing how much confidence can be placed in such a conclusion. Therefore, we need methods that incorporate error estimates into the assumption of a species' absence.

To that end, several models have been proposed. Green and Young (1993) discuss a model

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based on the Poisson distribution, which can be used to calculate the minimum sampling effort required to detect a rare species, given that the mean density per sampling unit (the Poisson parameter) is known. Solow (1993) presents a model for repeated sampling from a site where the time of the most recent sighting of a species is used as a test statistic. This model retrospectively estimates how much confidence can be placed in the hypothesis that a species has become extinct, given a sequence of negative findings.

Guynn et al. (1985), McArdle (1990), and Reed (1996) present a probability model to estimate retrospective confidence in detection, but which also may be used to address the prospective question of how many visits without observing a species are required to be statistically confident of its absence. To parameterize this model, the probability of detection of a species per visit is needed. To my knowledge, the probability of detection has never been estimated and used in this probability model for any species.

Here, I apply the probability model to data from 3 snake species to calculate the number of times a site has to be unsuccessfully visited to statistically establish the absence of these species. This is important, given the recently documented worldwide declines of reptiles (Gibbons et al. 2000). Snakes are notoriously difficult to detect (Rodda 1993) due to their small size, immobile and cryptic behavior, camouflaged color patterns, rarity, the inaccessibility of their habitats (e.g., cliff-faces, screes, tree cavities), and because they often are hidden in vegetation and underground. Nondetection of a snake species at an occupied site may result from at least 3 factors: (1) the snakes may be hidden in refugia, (2) they may be active on the surface but overlooked by the observer, or (3) a site may be temporarily unoccupied (Flatt et al. 1997). Thus, even at sites where they are present, it is possible that snakes are missed during a single survey.

In this paper, I estimate the probability of detection for 3 of the most widespread snake species in Europe (*Vipera aspis, Coronella austriaca, Natrix natrix*). I address the following questions: (1) What factors affect their probability of detection? and (2) How many surveys are required to demonstrate the absence of these species with 95% probability?

I use a generalized logistic regression model for sites known to support populations of these species. Because of their size and behavior, 2 species (*V. aspis* and *N. natrix*) are relatively easy to detect, while the third (*C. austriaca*) is less so. In addition to species-specific differences, probability of detection likely varies by habitat type and size, population sizes, and across seasons and years. Modeling the probability of detection allows us to test the effects of these factors and to obtain correct standard errors for the estimates. Based on the probability of detection, the minimum number of unsuccessful visits needed to determine a species' absence can be calculated with a given probability. This information can be used to judge the effectiveness of monitoring efforts and aid in the design of more successful approaches.

METHODS

The Model

The probability model presented by McArdle (1990) considers a number of sampling visits (N) to a site to detect a species that has a probability of detection (p) at any 1 visit. If we assume that the visits are all comparable and independent, the probability of not seeing a specimen after N visits is

$$\text{Probability } (N \text{ unsuccessful visits}) = \alpha = (1 - p)^N \quad (1)$$

We can then solve for N and get

$$\log(\alpha) = N \times \log(1 - p) \quad (2)$$

$$N = \log(\alpha) / \log(1 - p) \quad (3)$$

For $N\,min$, the minimum number of visits necessary before concluding a site is unoccupied, if we set a confidence level of 95% (and therefore $\alpha = 0.05$), we get

$$N\,min = \log(0.05) / \log(1 - p) \quad (4)$$

If we want a lower probability of misclassifying an occupied site, α can be taken as 0.01 (see also discussion in Reed 1996).

The only parameter necessary to compute $N\,min$ is the probability of detection p, which can be estimated empirically. We can estimate p from visits to sites known to be occupied if we assume that sites remain occupied during the entire study period, i.e., that there are no permanent population extinctions. This is reasonable given the short duration of the study.

Study Species

The poisonous asp viper (*Vipera aspis*) and the nonpoisonous smooth snake (*Coronella austriaca*) both reach an adult length of 50–70 cm. The nonpoisonous grass snake (*Natrix natrix*) reaches an

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adult length seldom exceeding 120 cm. *Vipera aspis* has a western European distribution (Saint Girons 1997), while *C. austriaca* and *N. natrix* are widely distributed between Spain and the Ural Mountains and Lake Baikal, respectively (Kabisch 1997, Strijbosch 1997). *Vipera aspis* and *C. austriaca* live in habitats with a southern aspect, abundant bushes and rocks or artificial stone structures, along the edges of forests and roads, and even within open forests that contain cliffs, screes, or clear-felled areas (Hofer et al. 2001). *Natrix natrix* feeds predominantly on amphibians and often is considered a wetland snake, but it also occurs in drier habitats frequented by the 2 other species. All 3 species are endangered in the study area (see Jäggi and Baur 1999 for *V. aspis*). The study sites represent the entire range of habitat types of *V. aspis* and *C. austriaca* in the study area, but only part of the habitat types of *N. natrix*. All 3 species are diurnal, active from March to October, and prefer warm and humid weather. Excessively low or high temperatures, low humidity of soil and air, strong wind, or strong rain inhibit their activity. Detailed information on the biology of the 3 study species can be found in Spellerberg and Phelps (1977), Engelmann (1993), Günther and Lehnert (1996), Monney (1996), Naulleau (1997), and Kabisch (1999).

Study Area

I studied snake sites from 1994 to 1998 between the towns of Besançon, France (47°15′N, 06°00′E), Pontarlier, France (46°55′N, 06°20′E), and Olten, Switzerland (47°20′N, 07°50′E), along an approximately 140-km stretch of the Jura Mountains (Kéry 2000). A snake site was defined as a patch of homogeneous habitat where a particular species was known to occur during the study. One population may have been divided into several sites according to discrete differences in habitat type. Knowledge about site occupancy was obtained from my own experience with *V. aspis* in the study area (M. Kéry, unpublished data) or from other herpetologists (see Acknowledgments).

I studied 62 *V. aspis*, 54 *C. austriaca*, and 52 *N. natrix* sites. The total number of study sites was 87, with ≥1 species often occurring at the same site. Sites were predominantly between 400 and 800 m in elevation and had a southern aspect (SW to SE). Sites were classified into 4 habitat types: woodland edges–roadsides, clifftops, screes, and habitats with artificial stone walls. The first 2 are fairly linear habitats, while the last 2 are more 2-dimensional. Most sites ranged from 10 to 400 m in length, with a few extending up to 1,600 m.

Field Methods

From 1994 through 1998, the 87 known snake sites were visited 645 times. During each visit, I followed Swiss governmental inventory protocols (e.g., Dusej and Billing 1991, Hofer 1991, Flückiger and Peltier 1999, Müller and Dusej 2000) and rapidly and completely searched suitable habitat for the study species. Searches took 5–60 min, depending on the size of the site. For each site, habitat type and size (the length of my search path) were noted. Linear sites (e.g., woodland edges) were searched completely, and so search length equaled size. Two-dimensional sites (e.g., screes) were checked along a geometrically irregular search path which remained the same for a site. To search for snakes, I walked slowly at an even pace and recorded each snake observation. Snakes were either seen basking or noticed when escaping. Because I walked at a constant pace across all of the sites, the length of the search path also is a measure of search effort.

Data Analysis

I first estimated probability of detection (parameter p in equations 1 and 4) from visits to snake sites where the species were known to be present and tested what explanatory factors were related to detection. I then entered the estimate of p into equation 4 to obtain the minimum number of necessary visits ($N\ min$).

Explanatory factors were 4 habitat types; 3 site size classes; 3 population size classes; 6 months (May–Oct); 5 years (1994–1998); and 62, 54, and 52 sites (for *V. aspis*, *C. austriaca*, and *N. natrix*, respectively). Site size corresponded to a search path per site of <150 m, 150–500 m, and >500 m. These limits were chosen arbitrarily to produce groups containing approximately equal numbers of sites. As a crude index of population size at a site, I used the maximum number of animals that I had seen per species and site on any 1 visit during the 5-year study period (3 classes: 0–1, 2–3, and ≥4 animals seen).

I modeled the relationship between probability of detection and various factors using a generalized linear mixed model (GLMM) with year and site as random effects (Breslow and Clayton 1993). Fixed effects were habitat type, size of site, snake population size, and the month during which the visit occurred. I tested fixed effects using Wald tests (Dobson 1990). I tested random

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effects using a likelihood ratio test by comparing 2 nested models with the same fixed effects; 1 model contained a variance component for the random effect and the other did not. The difference in deviance between the 2 models under the null hypothesis is approximately chi-square distributed on 1 df (Payne et al. 1993).

I first tested a model including the main effects and all 2-way interactions between the fixed effects. None of these interactions were significant among the 3 species. I then tested the model containing only the main effects. These results are presented in the analysis of deviance (Table 1).

To estimate the probability of detection, I chose a model containing only the statistically significant factors. The predicted means for population size (Table 2) and other significant factors are fitted proportions, adjusted with respect to the other fixed factors by averaging across their levels. This is analogous to least-square means produced in an ANCOVA. Furthermore, because none of the 2-way interactions were significant, it provides a valid summary of the effect of each factor (Mead 1988).

I used a GLMM rather than a conventional generalized linear model (GLM, or logistic regression; McCullagh and Nelder 1989) because of the 2-level structure of the data. Individual visits were clustered within the different sites. Only the fixed factor month was measured at the lower level, while the other fixed factors varied at the (higher) site level. A GLMM analysis is analogous to a split-plot ANOVA design and accounts for the clustering of observations (Littell et al. 1996). In the testing of factors associated with the higher level and the computation of the SE of their means, a GLMM correctly considers the additional variability between years and sites (Milner et al. 1999). I did similar analyses using a conventional GLM. These analyses yielded very similar estimated means for these factors, but misleading (i.e., too short) SEs. For a recent comparison of a GLMM with the conventional GLM, see Milner et al. (1999).

The minimum number of necessary visits per site (*N min*) was computed according to equation 4. Standard errors for the minimal number of necessary visits were obtained by adopting the suggestion by McArdle (1990) of plugging into equation 4 the estimate for the probability of detection ± 1 SE. All analyses were conducted using the statistical package GenStat 5.3.2 (Payne et al. 1993).

Table 1. Relationships between explanatory variables and probability of detection per visit for *Vipera aspis* (n = 472 visits), *Coronella austriaca* (n = 553 visits), and *Natrix natrix* (n = 523 visits) based on a generalized linear mixed model. Estimated variance components (SE): *V. aspis*: year effect = 0.330 (0.281), site effect = 0.929 (0.366); *C. austriaca*: year effect = 0.000 (0.079), site effect = 1.152 (0.665); *N. natrix*: year effect = 0.0199 (0.067), site effect = 1.267 (0.544).

Species	Source	df	χ^2	P
Vipera aspis	Habitat type	3	3.79	0.29
	Size of site	2	1.90	0.39
	Population size	2	22.00	<0.001
	Month	5	13.81	0.02
	Year variance component	1	0.0	>0.99
	Site variance component	1	27.0	<0.001
Coronella austriaca	Habitat type	3	10.96	<0.01
	Size of site	2	3.71	0.16
	Population size	2	15.12	<0.001
	Month	5	13.36	0.02
	Year variance component	1	0.0	>0.99
	Site variance component	1	78.0	<0.001
Natrix natrix	Habitat type	3	5.62	0.13
	Size of site	2	0.10	0.95
	Population size	2	7.90	0.02
	Month	5	21.06	<0.001
	Year variance component	1	10.00	<0.01
	Site variance component	1	249.00	<0.001

Table 2. Estimated mean probability of detection (p) per visit (with lower and upper bounds; ± 1 SE) for different population size classes of *Vipera aspis*, *Coronella austriaca*, and *Natrix natrix*. Estimates are derived from the generalized linear mixed model (GLMM) analysis in Table 1 and are based on the significant fixed effect factors only. They are predicted means averaged across the levels of the other factors. Standard errors (SE) in a GLMM are computed on the scale of the linear predictor and therefore are not symmetric around the backtransformed estimate. These SE correctly incorporate the variance components due to years and sites (see text for further details).

Species	Population size class	Probability of detection (p)	Lower bound of estimate	Upper bound of estimate
Vipera aspis	Small	0.23	0.17	0.31
	Medium	0.55	0.45	0.64
	Large	0.70	0.61	0.78
Coronella austriaca	Small	0.09	0.05	0.15
	Medium	0.45	0.30	0.62
	Large	0.56	0.40	0.71
Natrix natrix	Small	0.11	0.07	0.18
	Medium	0.25	0.16	0.36
	Large	0.25	0.16	0.36

RESULTS

From 1994 through 1998, 62 *V. aspis* sites were visited 472 times, with 350 animals recorded on 182 occasions. On average, each *V. aspis* site was

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visited 7.6 times, and on 39% of all visits, ≥1 animal was seen. I visited 54 *C. austriaca* sites 553 times, with 160 animals recorded on 84 occasions. On average, I visited each *C. austriaca* site 10.2 times, and on 15% of all visits, ≥1 animal was seen. I visited 52 *N. natrix* sites 523 times, with 114 animals recorded on 68 occasions. On average, I visited each *N. natrix* site 10.1 times, and on 13% of all visits, ≥1 animal was seen.

For *V. aspis*, probability of detection varied significantly among population size classes and among months (Table 1). Probability of detection was lowest in sites containing small populations of *V. aspis* (23%; Table 2), and much higher in medium and large populations (55% and 70%). Using equation 4, this translates into 12, 4, and 3 visits to small, medium, and large *V. aspis* populations, respectively, before it can be concluded with 95% confidence that the site is unoccupied (Fig. 1A). Seasonally, probability of detection was lowest during May and October (34% and 36%, respectively) and ranged from 51% to 63% during the remaining months during the activity period. No significant variation occurred between years.

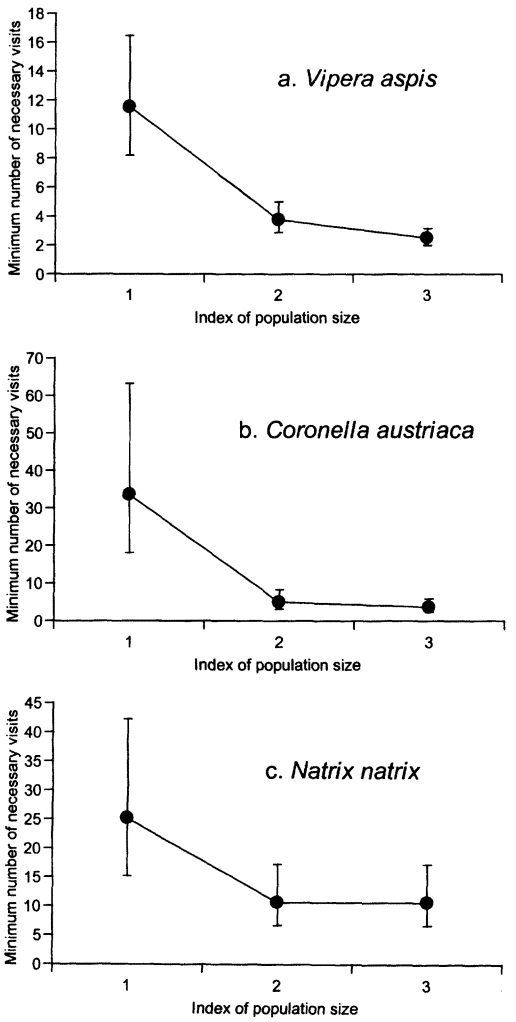

Fig. 1. Minimum number of necessary visits (including lower and upper SE bounds) to suspected sites with small, medium, and large populations of (a) *Vipera aspis*, (b) *Coronella austriaca*, and (c) *Natrix natrix*, before one can assume with 95% probability that a site is unoccupied. Values are based on the estimated probability of detection (p) given in Table 2. Note different scales of the ordinates.

For *C. austriaca*, probability of detection varied significantly among habitat types, among population size classes, and among months (Table 1). It was particularly low at sites containing small populations of *C. austriaca* (9%; Table 2), and much higher in medium and large populations (45% and 56%, respectively). This translates into 34, 5, and 4 visits to small, medium, and large *C. austriaca* populations, respectively, before it can be concluded with 95% confidence that a site is unoccupied (Fig. 1B). Probability of detection was highest on cliff faces (64%), followed by screes (33%), stone-wall habitats (23%), and woodland edges–roadsides (15%). Seasonally, probability of detection was lowest during October (6%) and ranged from 28% to 51% during all other months during the activity period. No significant variation occurred between years in the probability of detection of *C. austriaca*.

For *N. natrix*, probability of detection varied significantly among population size classes, among months, among sites, and among years (Table 1). Probability of detection was lowest in sites containing small populations of *N. natrix* (11%; Table 2), and marginally higher in medium and large populations (25% for both). This translates into 26, 11, and 11 visits for small, medium, and large *N. natrix* populations, respectively, before it can be concluded with a 95% probability that the site is unoccupied (Fig. 1C). Probability of detection was lowest during October (6%) and between 16% and 35% during other months.

The site variance components in the probability of detection were significant for all 3 species. Thus, site attributes other than population size class (*V. aspis* and *N. natrix*) and habitat type and population size class (*C. austriaca*) created among-site heterogeneity.

DISCUSSION

To statistically establish the absence or extinction of especially rare or elusive species from a

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site is an important but often neglected issue in both basic and applied ecological studies. To that aim, Guynn et al. (1985), McArdle (1990), and Reed (1996) proposed a model based on basic probability theory, which I applied to data from 3 snake species. I (1) review how well the assumptions of the model were met, (2) discuss conclusions specific to the biology of these snakes, and (3) consider what general conclusions can be drawn from this study with respect to other rare and elusive species.

Methodological Considerations

The probability model assumes that visits are independent and that probability of detection is stationary over time. During this study, a yearly average of only 1.5, 2.0, and 2.0 visits, respectively, were made to each of the *V. aspis, C. austriaca,* and *N. natrix* sites. Therefore, successive visits can be considered independent. On the other hand, the stationary assumption (McArdle 1990) is not strictly met, because probability of detection varied among months for all species and differed among years for *N. natrix.*

Predictions of the probability of detection (p) are based on averages of these time factors. McArdle (1990) shows that the minimum number of necessary visits (*N min*) estimated with a time-invariant p is an upper limit for the true value when p varies over time. Thus, when using a time-invariant estimate of the probability of detection to compute *N min*, one has a slightly higher confidence in the absence of a species than the nominal level of 95% ($\alpha = 0.05$).

Better estimates of *N min* to a specific new site with unknown occupancy status also could be computed (McArdle 1990). Using the logistic regression equations described in this study and the attributes of a new site (habitat type, suspected population size class) and of each visit (e.g., month of the visit), it is possible to predict for a series of visits to a new site the probability of detection p for a species for each individual visit i, yielding a set of p_i. For a given number of unsuccessful visits to this new site, the probability of that many unsuccessful visits could be calculated as the product of $(1 - p_i)$ over all visits.

Other factors that may potentially affect the detection probability of the snake species include radiation, temperature, humidity, soil dryness, and the physiological state of the animal. I did not quantify these in this study. It is likely that their effects are explained by summary explanatory variables such as year, month, and site. Because of the random visitation scheme of the sites, these effects also may have been evenly distributed across the levels of the factors studied and therefore amalgamated in the statistical error term. Thus, such unmeasured effects are unlikely to have biased the results.

One limitation of this study is that it is based on only 1 observer in 1 region. To make more general recommendations on how many times a site must be checked to infer the absence of snake species, variability among regions and observers in the probability of detection should be documented.

One result of this study is that it takes a large minimum number of visits to confirm that a species is not present at a site. Even an observer with twice my sampling efficiency would correctly identify only 45.8, 17.1, and 22.4% of sites with small populations of the 3 species *V. aspis, C. austriaca,* and *N. natrix,* respectively, on a single visit. The observer may still need many more visits to a site to produce a reliable answer about its status of occupancy.

For snake conservation efforts, the costs of Type II errors (i.e., not recognizing that a site is occupied by a species) may be high. A more stringent probability criterion can be used to lower the risk of Type II errors. If 99% instead of 95% confidence is desired in order not to miss a small population of *V. aspis, C. austriaca,* or *N. natrix,* respectively, as many as 18, 49, and 40 visits during the activity period may be necessary.

Biological Considerations

The major factors affecting probability of detection for all species were population size and season. Sites supporting a small population had a much lower probability of detection than sites containing a large population. Probability of detection was smaller during the months near the beginning and end of the annual activity period of the snakes. This could result from seasonal habitat use (e.g., some habitats used only during summer). Variation in probability of detection occurred during the summer months. This may be related to activity cycles such as molt, digestion, or gestation, when snakes are particularly dependent on solar radiation and therefore expose themselves more.

No effect of habitat type or year occurred for 2 of the species, and no effect of the size of a site for any species. This could suggest considerable generality, within species, in space and time of the results of this study. An alternative interpretation of the lack of a habitat effect could be the broad manner in which habitat types were

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defined. The lack of any effect of site size probably was related to masking by the strong effects of population size. Larger populations often were associated with larger sites. The significant variation of detection probability among sites in all 3 species means that other factors vary among them, such as vegetation cover or vegetation structure (Bibby and Buckland 1987), suggesting directions for future studies.

The 3 species varied considerably in probability of detection. *Vipera aspis* was the most detectable species across all population size classes, and *C. austriaca* was the least detectable in small populations. This confirms the experience of Swiss field herpetologists (e.g., C. Berney, Basel, Switzerland and T. Ott, Aarau, Switzerland, personal communications). However, *N. natrix*, generally regarded as a relatively conspicuous species, barely differed from the elusive *C. austriaca* in detectability in small populations, and actually had a much smaller detectability in medium and large populations. Part of this discrepancy may be explained by the selection of sites. The sample included more optimal *V. aspis* and *C. austriaca* sites, but few high-density *N. natrix* sites. Typical wetland sites of *N. natrix* with large populations likely would have increased the probability of detection for the large population size class considerably. However, any lack of truly large populations in the sample of sites cannot explain the low detectability of *N. natrix* in the small population size class. This suggests that where *N. natrix* occurs in small populations, it may be similarly elusive as the notoriously difficult *C. austriaca*. Note, however, that a small population size index is not directly comparable across species.

Specifically, 3 conclusions for these snake species can be drawn. First, the extent of occurrence of these elusive species may be grossly underestimated. For instance, in an inventory, few sites suspected to support small populations of *C. austriaca* or *N. natrix* are probably ever visited 34 or 26 times, respectively. Hence, many more sites might be occupied than is apparent from a survey subject to the usual constraints in terms of time and money. In addition, even at sites where these species are believed to be extinct, it may well be worthwhile to search further.

Second, in a survey of these species, unknown sites whose occupancy status is to be assessed probably are best assumed to be occupied by small populations. Large populations probably are known from the outset or will be detected anyway. If a species is suspected to have been extirpated at a site, but in reality is not, it probably only has a small population left. For a conservative estimate of the minimum number of necessary visits, it may therefore be best to use the estimates based on sites occupied by small populations. In this study, unknown sites suspected to contain a small population of *V. aspis*, *C. austriaca*, or *N. natrix* needed to be visited at least 12, 34, and 26 times, respectively, without recording any animal before it may be concluded with a 95% probability that they are not currently occupied. This is an order of magnitude higher than the typical 1–4 visits per site in most Swiss governmental inventories (e.g., Dusej and Billing 1991, Hofer 1991, Flückiger and Peltier 1999, Müller and Dusej 2000).

Third, to prove the presence of these species on a regional rather than a local scale, it may be more efficient to survey during some months and in some habitats than in others. All 3 species had a lower detectability near the end of the activity season. Thus, efforts at locating occupied sites during October, for example, may be wasteful. *Coronella austriaca* had the highest detectability in cliff habitats. Thus, to prove its occurrence in a region, this habitat type should receive sufficient sampling efforts.

MANAGEMENT IMPLICATIONS

Three general conclusions can be drawn from this study. First, it was possible to estimate the probability of detection in 3 typically elusive species. The ideas presented here can then be applied to any study of animals that are difficult to observe, and where the probability of detection may influence the results. In an inventory, for instance, the true number of occupied sites may be estimated more accurately. In an ecological study on habitat preferences based on sightings of the animals in the field, it is useful to determine whether detectability varies in different habitat types. If it does, then by knowing the relative detectabilities, the number of sightings in various habitat types can be weighted to yield a better estimate of true habitat preferences.

Second, to ascertain the presence of snakes and other animal species that are not easily seen, a much larger search effort may be necessary than is usually conducted. In governmental reptile inventories in Switzerland, for instance, surveyed sites have been visited a maximum of 4 times (e.g., Dusej and Billing 1991, Hofer 1991, Flückiger and Peltier 1999, Müller and Dusej 2000). Based on my estimates, a small population of *V.*

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aspis, *C. austriaca*, and *N. natrix* has a 35%, 69%, and 63% chance, respectively, of remaining undetected with only 4 visits. Hence, this procedure clearly is insufficient to produce reliable data about the complete distribution of these snake species and may miss many occupied sites. Landscape planning based solely on such inventories is bound to ignore many populations, especially small ones.

Third and finally, however, this does not mean that such inventories are useless as a basis for the conservation of the surveyed species. But, it is important to recognize their limits. For elusive species such as snakes, inventories should be viewed exclusively as proving the presence of a species at some sites. They must not be taken to infer absence at any site where a species has not been found. It may never be possible to check all the sites during such an inventory 34 times, for instance (the estimated minimum number of necessary visits to detect a small *C. austriaca* population). Therefore, if a species is known to occur in a region, its presence at a given suitable-looking site or at a site that has been occupied before should be assumed for as long as there is no evidence to the contrary. If, for instance, there are any construction plans at such a site, the onus should be on the builder to provide that evidence, i.e., to commission (and finance) an experienced field herpetologist to visit the site 34 times. This amount of effort is obviously not feasible for all sites in an entire inventory. However, we should make it a top priority to conduct such surveys during the specific development planning for a given site. If not, we run the risk of losing rare and endangered species.

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